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Flexible alarm calling in meerkats: the role of the social environment and predation urgency

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Abstract: Flexible vocal production has been demonstrated in several vertebrate species with much work focusing on the role of the social “audience” in explaining variation in call production. It is, however, likely that the decision to call is an emergent property of both external and internal factors and the extent to which these factors are integrated has been little investigated. We addressed this question by examining the production of alarm calls in wild male meerkats (*Suricata suricatta*) in different social environments and different predator-encounter contexts. Males searching for reproductive opportunities (rovers), were followed: (i) in their home group and when prospecting, either (ii) solitarily, or (iii) in a coalition with other males. Results showed conspecific presence influenced the production of flee-alarm and recruitment calls. Solitary rovers were less likely to produce flee-alarm calls compared to when with conspecifics, whether coalitionary rovers or the rover’s home group. Experimentally elicited recruitment calls were also produced less when males were solitary than when in their home group. Bark vocalisations, emitted when meerkats were safe were always produced, irrespective of conspecific presence, indicating these calls function to address predators. The probability of producing flee-alarms also increased with urgency of the predation event. Our results indicate that variation in alarm call production depends on whom the call is addressed to, and also the motivational state of the caller. We argue that neglecting to integrate internal and external factors when elucidating mechanisms underlying vocal production can potentially lead to misguided, parsimonious conclusions regarding vocal flexibility in animals.

DOI: <https://doi.org/10.1093/beheco/ars129>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-72017>

Journal Article

Published Version

Originally published at:

Townsend, Simon; Rasmussen, Maria; Clutton-Brock, Tim; Manser, Marta (2012). Flexible alarm calling in meerkats: the role of the social environment and predation urgency. *Behavioral Ecology*, 23(6):1360-1364.

DOI: <https://doi.org/10.1093/beheco/ars129>

Original Article

Flexible alarm calling in meerkats: the role of the social environment and predation urgency

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Flexible vocal production has been demonstrated in several vertebrate species, with much work focusing on the role of the social “audience” in explaining variation in call production. It is, however, likely that the decision to call is an emergent property of both external and internal factors, and the extent to which these factors are integrated has been little investigated. We addressed this question by examining the production of alarm calls in wild male meerkats (*Suricata suricatta*) in different social environments and different predator-encounter contexts. Males searching for reproductive opportunities (rovers) were followed 1) in their home group and when prospecting either 2) solitarily or 3) in a coalition with other males. Results showed that conspecific presence influenced the production of flee-alarm and recruitment calls. Solitary rovers were less likely to produce flee-alarm calls compared with when they are with conspecifics, whether coalitionary rovers or the rover’s home group. Experimentally elicited recruitment calls were also produced less when males were solitary than when in their home group. Bark vocalizations, emitted when meerkats were safe, were always produced irrespective of conspecific presence, indicating that these calls function to address predators. The probability of producing flee alarms also increased with the urgency of the predation event. Our results indicate that variation in alarm call production depends on whom the call is addressed to and also on the motivational state of the caller. We argue that neglecting to integrate internal and external factors when elucidating mechanisms underlying vocal production can potentially lead to misguided, parsimonious conclusions regarding vocal flexibility in animals. **Key words:** alarm calls, audience effects, meerkats, predation urgency, social environment. [*Behav Ecol*]

INTRODUCTION

When encountering predators, it is vital that animals respond correctly to improve survival probabilities. Alarm calling is one such antipredator strategy that, when performed reliably, improves escape responses to predators and hence ultimately the chances of survival (Marler 1967). However, such vocal defense also comes with an intrinsic cost, given that producing alarm calls can increase the risk of being detected by a predator (Sherman 1977; Hoogland 1996). To mitigate the costs associated with alarm calling, it would be advantageous to emit vocalizations flexibly depending on the potential benefit likely to be accrued. A number of studies over the past 4 decades have shown that animals are capable of adjusting the use of alarm calls depending on the surrounding social environment. From vervet monkeys (*Chlorocebus pygerythrus*) to yellow mongoose (*Cynictis penicillata*), mammals will not alarm call in the absence of conspecifics (Cheney and Seyfarth 1985; Le Roux et al. 2008). Further evidence for more subtle audience effects suggests that the “composition” of the audience itself is also important. Belding ground squirrels (*Urocitellus beldingi*) and female vervet monkeys modify their alarm calling behavior based on the presence of kin (Sherman 1977; Cheney and Seyfarth 1985), whereas male vervets and Thomas langurs (*Presbytis*

thomasi) pay more attention to the presence of adult females (Cheney and Seyfarth 1985; Wich and deVries 2006). Similar results have been described for group-living birds such as downy woodpeckers (*Picoides pubescens*) (Sullivan 1985) and domestic chickens (*Gallus gallus*) (Marler et al. 1986).

Audience effects are of particular interest, first because they suggest that animal vocal production does not purely rely on a hardwired stimulus response-based mechanism but instead that animals have considerable control over when to produce their species-specific calls (Marler et al. 1986; Karakashian et al. 1988; McGregor 2005; Zuberbühler 2008). Second, flexible calling behavior additionally implies that animals attend to the social composition of the groups in which they reside (Wich and deVries 2006) and integrate this information in potentially strategic ways, possibly even based on the assessment of how individual receivers may process this information (Slocombe and Zuberbühler 2007). Audience effects therefore represent one potential method to assess what animals understand about their surrounding social worlds (Tomasello and Call 1997; Cartmill and Byrne 2007; Zuberbühler 2008; Townsend et al. 2008).

To date, most of the empirical studies addressing the effect of the audience have focused on alarm calling in the context when escape responses are beneficial, such as during flee-alarm calls, and less in the context of recruitment of other group members for inspecting predator cues or indeed mobbing a predator. Furthermore, previous work has not integrated the potentially additive effect of predation urgency into the conceptual and empirical framework surrounding socially mediated alarm calling behavior. This is a particularly important point because it is plausible that the influence

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Received 23 February 2012; revised 8 July 2012; accepted 21 July 2012.

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imposed by the caller's audience may, at times, be overridden by the current risk or urgency experienced by individuals. Omitting this internal, motivational factor may lead to premature conclusions regarding, in particular, the absence of flexible calling behavior (see Tomasello 2008). Through employing both observational and experimental methods, we investigated how the alarm calling behavior of prospecting male meerkats (*Suricata suricatta*) was affected by the social environment and the urgency level of the situation.

Meerkats are diurnal, cooperatively breeding mongooses, which live in groups of up to 50 individuals (Clutton-Brock et al. 2005). They rely heavily on vocal communication as a means to coordinate group behavior (Manser 1998; Bousquet et al. 2011; Townsend et al. 2011) and, as a consequence of intense predation pressure, have evolved a sophisticated functionally referential alarm call system, which denotes not only the predator type but also the level of urgency (Manser 2001; Manser et al. 2001). Since reproduction is typically restricted to a dominant pair, adult subordinate males regularly conduct extraterritorial forays to mate with females of other groups and potentially assess dispersal opportunities (Doolan and Macdonald 1996; Young et al. 2007; Mares et al. 2011). These males either prospect solitary or in small groups with other males of their natal or foreign groups, called coalitions (Young et al. 2007). Coalition rovers prospect mostly as cohesive groups, showing some cooperative behavior such as guarding, but they do not actively support each other during fights. Extraterritorial forays therefore provide an ideal opportunity to investigate the vocal behavior of meerkats in antipredator situations when exposed to different social contexts.

We investigated the alarm calling behavior of meerkat males in different social environments, that is, when foraging in their home group, when prospecting as single individuals, or when in coalitions. In particular, we addressed the following two questions: 1) Does the social environment influence the production of 3 different alarm call categories typically related to different predation contexts: a) flee-alarm calls; b) recruitment calls, c) potentially predator-directed barks; 2) Does the production of alarm calls depend on the urgency level of a predator encounter? To ensure that the type of audience, and not the context of prospecting forays, leads to a modification in alarm calling, we compared the calling behavior of the same meerkats in different contexts, such as prospecting solitary or in coalitions, and also when in their natal group. If meerkats are flexible in adjusting alarm call emission depending on the social environment, we predicted that single rovers should decrease their production of conspecific-directed flee-alarm calls and recruitment calls during natural predation events and when experimentally presented with secondary predator cues. For bark calls, if their function is to address the predator and signal that it has been detected, we predicted no effect of social environment. Furthermore, rovers in coalitions should not differ in their natural calling behavior in comparison to when residing in their home group. However, whether roving singly, in coalitions, or when in home groups, we also predicted an increase in the proportion of alarm calls emitted during more urgent predator encounters, when, for example, exposed to a dangerous predator at a close distance.

MATERIALS AND METHODS

Study population

We studied a wild, but habituated population of meerkats at the Kuruman River Reserve in South Africa. The study site is situated in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E) (Clutton-Brock et al. 1998; see Russell et al. 2002 for details on topography,

vegetation, and climate). Observations and experiments were performed between August 2005 and January 2006 with some additional dog urine presentations in January 2007. Group size ranged from 13 to 41 animals. All meerkats were habituated to close observation and handling, enabling detailed recordings of behavioral and acoustic interactions. Additionally, all meerkats were dye-marked and had a microchip transponder for individual identification. One individual in each group was fitted with a radio collar (Sirtrack®) to track the group at any time of the day (Jordan et al. 2007). The study population has been observed since 1993, and the life history of all individuals is known since birth. The study was conducted under the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa.

Audience categories and data collection

The social context a meerkat could experience was partitioned into 5 audience categories (Table 1). Rovers could prospect alone ("single") or in a group of 2–4 individuals ("coalition"). Moreover, we noted whether rover(s) prospected at a foreign group ("FG") or whether no group was close by ("NG"). Rovers with "no group close by" included individuals leaving their own group or the foreign group. The time a focal animal left a foreign group was defined as the point when foreign individuals were no longer encountered and the focal animal moved in the direction toward its own group territory. Rovers were followed for as long as possible, including the resting period during the warm midday hours. Instances when rovers returned to their own group were excluded from analyses due to a low number of predator encounters. All individuals that had been followed as rovers were additionally observed when they were within their home group. Since the hormonal and conditional state of males changes during prospecting forays (Young 2003), data in the home group were collected at least 3 days after a prospecting event. These males were followed for 3 h after leaving their morning sleeping burrow. In the afternoon, they were located by radiotracking (Receiver: ICOM R10) and observed until they disappeared into their sleeping burrow at sunset. Observations in the home group were stopped whenever the group interacted with foreign individuals.

Flee-alarm calls and the level of urgency

Seventeen single rovers were observed during 44 forays and 18 coalition rovers during 41 forays over a period of 470 h. When following a coalition of rovers, only 1 focal individual per prospecting event was observed. Data on alarm calling rate (number of predator encounters eliciting a vocal response/total number of predator encounters) were recorded with a handheld organizer (Psion organiser II, Model LZ64). During natural predator encounters we recorded the following: the predator type, the distance to the predator, the response of the focal animal, and the response of other meerkats nearby. Six distinct flee-alarm call types have been identified depending

Table 1
Prospecting males (rovers) were compared between 5 social contexts, coded 1–5

	Single	Coalition
No group close by ("NG")	1	2
At the foreign group ("FG")	3	4
In their home group	5	

on the type of predator (aerial or terrestrial) and the level of urgency (low, medium, and high urgency, see Manser 2001). All flee-alarm calls were included in the main analysis and to avoid pseudoreplication by including several responses for the same predator, only the strongest response was considered.

To test whether meerkats showed a different vocal behavior depending on the danger of the situation, both the type of approaching animal and the distance to it were considered. Approaching animals were either predators such as carnivores and raptors or nondangerous herbivores, birds, and vultures (Manser 2001). The distance was categorized as “close” when birds were less than 200 m away and terrestrial animals were less than 50 m away. A predator encounter was regarded as highly dangerous when a predator was considered to be close, whereas a nondangerous animal far away was regarded as a low threat. Any other combination of predator type and distance to the predator was regarded as a medium threat.

Recruitment calls to secondary predator cues

To investigate calling behavior in the context of recruitment, presentation experiments with secondary predator cues were performed. Dog urine from 8 different dogs was presented to investigate whether single rovers ($n = 10$) also emit recruitment calls, naturally elicited by secondary predator cues (Manser 2001). Dog urine was organized from a veterinarian and deep-frozen for a maximum of 14 days. Three milliliters of dog urine was mixed with sand in a Petri dish and presented on a 10×10 cm cardboard within 5 min. The reaction to the stimulus was filmed using a Sony digital video camera (DCR-TRV33E PAL). Identical presentations were performed on the same males (with the urine of the same dog) when they had returned to their home group. Although this might have caused an order effect, it was necessary to avoid any experiments that could not be used because the test individual would never act as a rover or would only begin roving after a long time period following the experimental manipulation in the group. To avoid habituation and any potential carryover effects due to experimental order, control presentations were carried out at least 1 week after the first urine presentation performed during roving events.

Bark calls

In situations where the predator is within a close proximity (raptor perched in tree, terrestrial predator) and the meerkats are at sheltered safe location, meerkats typically emit “bark” calls (Manser 1998), which differ from the other flee-alarm calls and recruitment calls included in our analyses. We compared the production probability of these bark calls from sheltered single rovers ($n = 6$) and groups of meerkats ($n = 30$ observations in 11 groups) over a period of 13 years (1995–2008, Manser long-term data set).

Statistical analysis

Generalized linear mixed-effects models (GLMMs) with a binomial error structure were used to investigate how both the audience and the urgency of the predation event affected meerkat alarm calling behavior. Because in these analyses the data were partially crossed (i.e. not every rover contributed to each of the audience categories) and we had repeated sampling from the same individual, we fitted “individual” as a random factor (Crawley 2002) by conducting random intercept models using the package lme4 (Bates and Maechler 2009). We first constructed the full model with the explanatory factors and their interactions (Urgency and Audience category) and tested the overall significance of the full model against a

reduced model (without the factors of interest) using a likelihood ratio test. Post-hoc GLMMs were used to investigate pairwise differences between the audience categories, and a sequential Bonferroni correction was applied to correct for multiple comparisons (Holm 1979).

The response to presentations of dog urine was analyzed using a binomial test for equality of proportions with a continuity correction. To compare production of alarm barks between solitary rovers and individuals within their home group in the presence of perched aerial predators or close by terrestrial predators, we coded the data into a binary variable. If no barks were produced during these situations, meerkats were allocated a 0 and when at least one bark was produced a 1 was allocated. We then performed an exact sign test to analyze the effect of audience presence on alarm bark production. All statistical tests were performed in R version 2.12.2 and SPSS V13.0/19.0, were 2-tailed, and were considered to be significant at $\alpha \leq 0.05$ or at the sequential Bonferroni correction level when it applied.

RESULTS

Emitting flee-alarm calls depends on audience categories and level of urgency

The probability to emit a flee-alarm call depended on the presence of conspecifics and the level of urgency of a predator encounter (Figure 1). The presence of conspecifics stimulated the production of alarm calls (GLMM, LR = 19.7, $df = 4$, $N = 130$, $P < 0.001$), with an increase in alarm calling probability from single rovers to coalitions of rovers and again to when the same rovers were in their home group. Single rovers, both away from their group (NG) and close to a foreign group (FG), were less likely to emit alarm calls compared with when observed in their home group (post-hoc GLMMs, single NG—home group: LR = 18.0, $df = 1$, $N = 61$, $P = 0.001$; single FG—home group: LR = 11.18, $df = 1$, $N = 73$, $P < 0.001$). Similarly, coalition rovers at a foreign group tended to emit fewer alarm calls than when recorded within their home group (post-hoc GLMM, coalition FG—home group: LR = 3.83, $df = 1$, $N = 71$, $P = 0.05$, adjusted Bonferroni alpha level: 0.01), whereas no such tendency was found when coalition rovers were not close to any groups

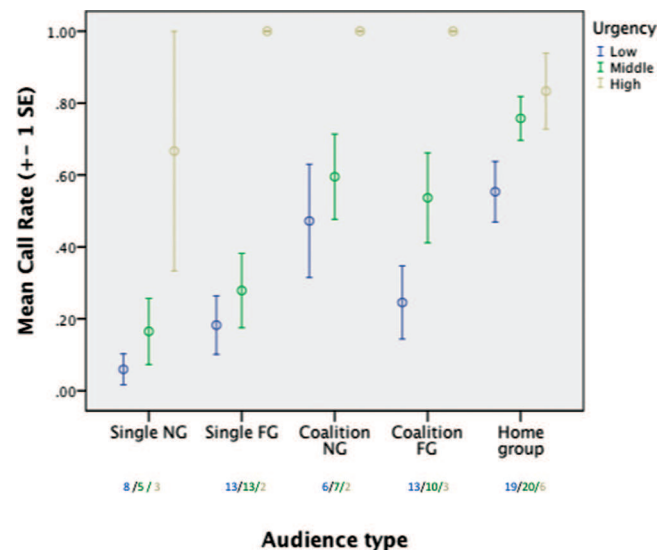


Figure 1
Mean alarm call rate in the different audience categories depending on the level of urgency of the situation (mean \pm 1 SE). Numbers indicate sample sizes for each urgency level and social context.

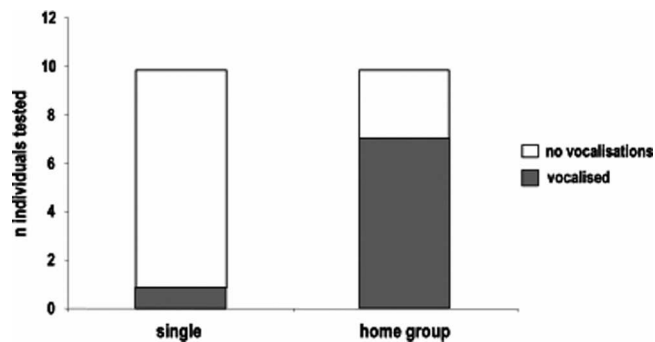


Figure 2
Males ($n = 10$) vocalizing to dog urine presentations depending on audience present (home group) or not (single).

(post-hoc GLMM, coalition NG—home group: LR = 0.33, $df = 1$, $N = 60$, $P = 0.56$). Within the audience categories, level of urgency of a predator encounter also affected alarm calling behavior in the same way in all social contexts. The higher the urgency level of a predator encounter, the more likely individuals were to emit alarm calls (GLMM, LR = 18.9, $df = 2$, $N = 130$, $P < 0.001$, see Figure 1). The interaction between urgency levels and audience categories was not significant (GLMM, LR = 3.7, $df = 8$, $N = 130$, $P = 0.87$).

Recruitment to secondary predator cues

When presented with dog urine as a secondary predator cue, single rovers were less likely to emit recruitment calls compared with when they were within their home group (Binomial test: $\chi^2_1 = 5.21$, $n = 10$, $P = 0.022$, Figure 2). Furthermore, the single rovers that did vocalize differed in their vocal behavior to the typical recruitment calling of individuals in their group. When single rovers produced recruitment calls, only ever 1 call was emitted, whereas in the group they emitted a series of calls from few seconds up to a minute (unpublished data).

Bark calls

In situations where the predator was close by (terrestrial or aerial) and the meerkats were at a safe place next to shelter, solitary rovers and individuals within their group emitted “bark” calls. Six single rovers were all observed emitting bark calls over long periods on such occasions, and groups of meerkats ($n = 30$ observations from 11 groups) also showed identical behavior, where 1 or several group members barked over long periods in the direction of the predator when sheltered. An exact sign test showed that there was no significant difference in alarm bark production between solitary rovers and groups of meerkats (2-tailed exact sign test: $P = 1.0$).

DISCUSSION

Solitary prospecting rovers were less likely to vocalize during predator encounters than coalition rovers, who instead showed a similar alarm calling behavior to that when residing in their home group. Furthermore, when experimentally simulating the presence of a predator, solitary rovers attempted to recruit less with recruitment calls than when they were presented with the same stimulus, but in their home group. Withholding alarm calls, whether flee alarms or recruitment calls, when solitary can ultimately reduce the risk of attracting a predator’s attention, which has crucial fitness consequences. When confronted with a perched aerial or close by terrestrial predator, solitary meerkats at a safe place were as likely to emit alarm bark vocalizations as individuals residing within their home group. These data therefore

support the idea that these calls are used to address the predator rather than to warn other group members of an imminent danger. In this context, it is likely that the better strategy is to advertise to the predator that it has been detected and to potentially encourage the predator to leave the area (Zuberbühler et al. 1999).

When meerkats have the opportunity to rove with other males, alarm calling rather than remaining silent provides benefits to the caller, in terms of alerting nearby conspecifics to potential danger, and likely prolongs the survival of other group members on whom the caller may currently be relying. Besides the audience of own group members (typically kin), the audience of extra-group foreign meerkats (typically non-kin) also influenced the alarm call behavior of roving individuals in predator encounters. Coalition rovers, for example, tended to vocalize less when close to foreign groups, though this result has to be taken with caution, given its significance level when corrected for multiple comparisons. In contrast to lone rovers, coalition rovers are faced with a trade-off to either warn their coalition partners of an approaching danger or to remain silent and not to reveal their presence to a nearby foreign group. Coalition rovers at a foreign group therefore might have acted selfishly not to be detected by the foreign group and to avoid fights with native males, as they can lead to severe injuries or even end lethally (Young et al. 2005).

These results support the hypothesis that meerkats are able to modify their alarm call production depending on the surrounding social environment and that not simply the context or a different motivation during prospecting forays is responsible for differences in the vocal behavior. Such “audience effects” on the production of alarm calls have been found in several other species (for recent reviews, see Zuberbühler 2008; Fichtel and Manser 2010). Given the seemingly widespread occurrence of this ability across the animal kingdom, from birds to nonprimate mammals and primates, it is likely that such a basic socio-cognitive ability is a product of convergent evolutionary processes (Fitch 2010).

Exactly what these results can tell us about the underlying social intelligence of meerkats is however unclear. For example, whether flexible alarm calling is purely a learned behavior or whether meerkats have some understanding with regard to how their vocalizations will influence receivers cannot be directly addressed by our findings. What we can tentatively infer is that not just the presence or absence of an audience influences meerkat alarm calling but also potentially the subtle differences in the composition of the audience, with audience familiarity further influencing the decision of roving coalitions to call. Future work is necessary to clarify to what extent the social context is integrated into the production of meerkat vocalizations, which will in turn help elucidate how fine grained meerkats’ social knowledge actually is.

Independent of the audience, the probability to emit alarm calls additionally varied depending on the threat level of a predator encounter. Meerkats were more likely to emit alarm calls when the risk level of encountering a predator was higher. This suggests, in part, that the meerkats assess the risk of predation before responding, which could further minimize the costs of producing alarm calls through avoiding interrupting foraging when this is not necessary. However, the arousal when detecting a predator might also have an impact on the production of alarm calls, as an increase in risk level often elicited a vocal response in single rovers when no conspecifics were around. This may indicate that in high-urgency situations animals have less control on their vocal production, as they may be under pressure to immediately respond.

A number of studies to date have suggested that either animals are able to control their vocalizations or their vocal production is a result of the underlying emotional state (Marler 1985; Cheney and Seyfarth 1990; Seyfarth and Cheney 2010). Examples of emotionally driven, inflexible alarm calling

behavior, in combination with the apparently ridged acoustic structure of calls, have since been invoked as partial evidence against a vocal route to human language evolution (Tomasello 2008). Our findings demonstrate that in fact these underlying production mechanisms initially eliciting the call might be intimately related and should not necessarily be seen as two juxtaposed alternatives. Indeed it is very plausible that the nature of the surrounding audience may well change the internal arousal of individuals, which in turn influences their vocal behavior. These results emphasize the need for future studies to also account for the relative urgency of predation events when investigating the flexibility of alarm calling behavior in animals. Such considerations may help to better clarify the role of the social environment in affecting alarm production and avoid obtaining false-negative results by, for example, only considering alarm calling during high-urgency predation events.

Together our results indicate that a substantial degree of flexibility underlies the alarm calling behavior of male meerkats. Such findings provide further support for the idea that animals as vocalizers are not robotic and ridged in their production of calls but are capable of modifying them based on the benefits that are likely to be gained from the current context. Furthermore, these results suggest that the mechanisms guiding alarm call production likely integrate both internal motivational and external social factors together, and hence it is important to look at these factors as mutually nonexclusive. Future work focusing on vocal production in social as well as solitary species, in the context of antipredator behavior or potentially other social contexts such as food advertisement or calls for social support, will help to elucidate how plastic the vocal system in animals really is.

FUNDING

University of Zurich.

We are grateful to the Kalahari Research Trust (Kuruman River Reserve) and surrounding farmers, in particular Family Hennie Kotze, for the permission to work on their land. We are also grateful to Johan Du Toit and Martin Haupt at the Mammal Research Institute, University of Pretoria, for logistical support. Many thanks go to all the volunteers and researchers at the Kalahari Meerkat Project for helping calling in rovers. Robert Seyfarth, an anonymous reviewer, Krys Golabek, Linda Hollén, Lorenz Gyax, Hansjoerg Kunc, Christophe Bousquet, Ines Braga Goncalves, and the Communication & Cognition VHB/ZH group provided helpful discussions and improvements on earlier drafts of the article.

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